

NEW MATERIAL OF THE EARLY TETRAPOD *ACANTHOSTEGA* FROM THE UPPER DEVONIAN OF EAST GREENLAND

by J. A. CLACK

ABSTRACT. New material of one of the oldest known tetrapods, *Acanthostega gunnari*, is described: three skulls, together in one block, in association with postcranial material. This is the first postcranial material to be described for *Acanthostega*. The skulls show an animal with a broad, closed, denticulated palate in which the pterygoids meet in the mid-line as in loxommatids and *Ichthyostega*. The ventrally grooved parasphenoid resembles that of some osteolepiform fish rather than that of tetrapods. The basal articulation is tetrapod-like with well-developed basiptyergoid processes. The otic capsules appear to be well ossified and the braincase fits flat under the skull table, in contrast to the complex facets in *Ichthyostega*. No synapomorphies with any particular tetrapod group have been discovered, but one additional character defining all tetrapods (large ornamented interclavicle) and two defining all neotetrapods (presplenial-anterior coronoid suture, surangular contributes significantly to margin of adductor fossa) have been identified. The latter two can be used to establish whether isolated lower jaws belong to fishes or to tetrapods.

THE earliest tetrapods yet known have been found in rocks of Upper Devonian (Famennian) age. They have now been recorded from several continents, including Australasia (Campbell and Bell 1977; Warren *et al.* 1986), South America (Leonardi 1983), and Eurasia (Lebedev 1984), but by far the largest number and best-preserved specimens derive from East Greenland. Tetrapods were first recognized there in 1931 during a series of expeditions led by Lauge Koch. The majority of described specimens from these expeditions pertain to the genus *Ichthyostega*, one has been placed in a second, related, genus *Ichthyostegopsis* (Säve-Söderbergh 1932), while two pertain to a third genus, *Acanthostega* (Jarvik 1952).

Ichthyostega and *Ichthyostegopsis* were first described in a preliminary report by Säve-Söderbergh (1932), who unfortunately died before being able to carry out the work more completely. His report gave basic descriptions of the skull roofs of several specimens, to many of which he gave separate specific names. Further information about *Ichthyostega* was published by Jarvik (1952), including details of the fish-like tail, the vertebral column, the hindlimb, the unique overlapping ribs, and new reconstructions of the skull and of the whole animal. The skull was shown to have many unusual features including apparently advanced ones such as the lack of an intertemporal and fused postparietals, and primitive ones such as a braincase retaining the ventral cranial fissure with the otic capsule not underlain by the parasphenoid. Jarvik (1965) gave more information on the limbs, with reconstructions of the pelvic girdle and the pectoral limb following in 1980. *A. gunnari* is known so far only from the skull roof in two specimens. A possible third specimen mentioned by Jarvik (1952) is not now included in this genus (Jarvik, pers. comm.).

The material to be described here was collected in 1970 during one of a series of expeditions led by Dr Peter Friend, then of the Scott Polar Institute, now of the Department of Earth Sciences, University of Cambridge (Friend *et al.* 1983). The fossils were collected by John Nicholson (Friend *et al.* 1976), as a secondary casual activity, the main objective being to draw up stratigraphic sections. Fossils from each collecting site were grouped under one 'lot' number prefixed G, and each item was also numbered separately.

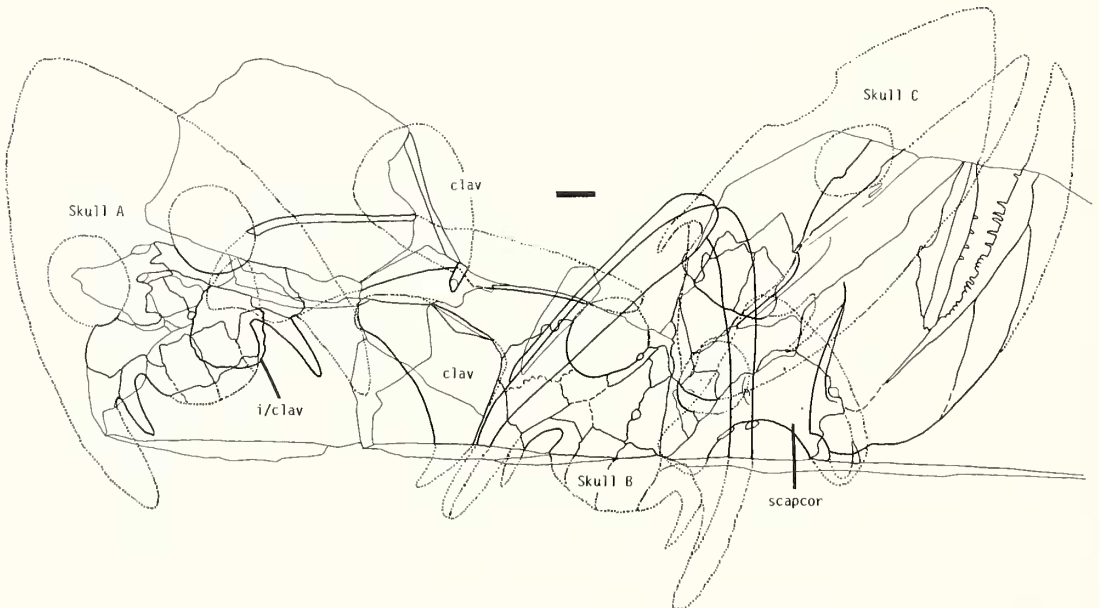
Tetrapods were found at three sites during the series of expeditions: G656, G680, and G920. The latter site, visited on 11 August 1970, yielded by far the bulk of the tetrapod remains, consisting

of many isolated elements, gathered as it was from scree on the mountainside. However, much of the great value of this material comes from the fact, which I have subsequently discovered, that many of the items from site G920 fit together to form one composite block. The cranial material is identifiable as belonging to the poorly known *A. gummari*. The associated postcranial elements in the block may be attributed to this form with reasonable confidence, though not those on isolated blocks. This material therefore more than doubles the known specimens of this form, substantially increases our knowledge of its anatomy, and indicates a new locality.

MATERIALS AND METHODS

Nicholson's site G920 is located on the south-east slope of Stensiös Bjerg, and derives from the top of the Britta Dal Formation. Material from this site consists of both isolated and associated cranial and postcranial elements, most of which are preserved in a weathered reddish-grey micaceous sandy siltstone, which is irregularly bedded. A few specimens are from a harder and more finely laminated greyer, but still micaceous, sandy siltstone, and are clearly from a different bedding plane. Bands of calcite are found both in this and in the redder rock, several fragments having a calcite lining along one edge.

In most instances, the bone is heavily weathered and preservation is often poor. Dermal bone is usually split through the middle spongy layer and the outer layer of dermal ornament often lost. Where endochondral bone has been exposed to weathering, the inner spongy bone is often reduced to a soft caramel-like substance. In other places it appears that chemical interchange has occurred between the bone and matrix, areas of apparently rotted bone having become coarse and crystalline, some of which has subsequently weathered to a powder. The matrix formed by the reddish-grey sandy siltstone is highly variable in character. The outer layer of weathered rock is usually soft and easily removed mechanically. In other places, the bone is covered by a thin layer of very fine- and even-grained red haematitic matrix which is so soft as to be removable with a stiff brush or fine pin. In other places the matrix is hard, coarse, and crystalline with much pink calcite, which differs little in colour from the outer layer of bone which is slightly browner in tone. The calcite



TEXT-FIG. 1. *Acanthostega gummari* Jarvik. Diagram of composite block UMZC T1300 to show distribution of elements. Scale bar, 10 mm.

crystals often adhere firmly to the bone, making preparation extremely difficult in these places. The bulk of this matrix had to be removed by careful use of a pneumatic pen or dental mallet, but removal of the final layer required the use of a very fine, frequently sharpened mounted needle, individual crystals being picked or scraped off to avoid damage to the bone. The matrix contains many mica flakes, sometimes lying over the bone, and here they help separation of bone and matrix. Many fragments of broken bone and scutes add to the difficulty of preparing and interpreting this material.

The material consists of a composite block (text-fig. 1) about 280 mm in length containing remains of three skulls, an isolated premaxilla, a lower jaw, two clavicles, an interclavicle, and a scapuloecoracoid. One skull (skull A, University Museum of Zoology, Cambridge (UMZC) number T1300*a-c*) (text-fig. 2) consists of the skull table with both tabular horns complete, part of the interorbital region and portions of the squamosals. Most of it is exposed in dorsal view, but the surface ornament has been eroded away except on the tabular horns which were exposed by mechanical preparation. The second skull (skull B, UMZC T1300*d-h*) (text-fig. 3) is essentially complete except for the suspensorium on each side. A section through the skull can be seen posteriorly, where the specimen is broken obliquely. The posterior part of the skull roof is preserved in ventral view on the counterpart of the specimen, while some of the snout region has been exposed in dorsal view by mechanical preparation. The lower jaws have remained *in situ* and the skull has been little disturbed except for flattening.

The third skull (skull C, UMZC T1300*f*) (text-figs. 4 and 5) cannot be certainly identified as *Acanthostega*, but is attributed to that genus on the grounds of its association with the other material in the same block, and it also has the posteriorly convex margin to the postparietals seen in *Acanthostega*. It provides an unusual view: the right side including the cheek and lower jaw has been folded underneath and most of the skull roof except for the posterior part of the postparietals has been lost. This has exposed what remains of the braincase and palatoquadrate in dorsal view. Both lower jaws remain attached to their respective quadrates, the left being more or less completely exposed in external view. The right lower jaw has lost its lateral (external) face so that the bones of the mesial face are exposed in lateral (internal) view. A section through the anterior part of the skull is visible where the snout has been lost (text-fig. 5c). This skull is associated with cervical elements and three ribs.

Other recognizable elements on isolated blocks include three skull table fragments, a frontal-prefrontal unit, part of an articular, portions of dentary and maxilla, an isolated lower jaw and humerus, a clavicle, two interclavicles, and a pelvic girdle. These cannot be assigned taxonomically at present.

Before preparation, the specimens were photographed and the more important cast in silastic (Silastomer RTV 9161), which was also used to provide a backing during mechanical preparation. Sections were provided where the calcite lining of the composite block could be removed mechanically and the section polished using fine-grade carborundum paper. The specimens are now registered as UMZC T1291-T1302.

In addition to the material discovered by Nicholson, I have been able to examine specimens of *Ichthyostega*, the holotype of *A. gummari* (GM A33), the second specimen (GM A85), and two other unidentified skull specimens (GM A88, GM A90), collected by the Danish-Swedish expeditions.

Abbreviations used for institutions: GM, Geologisk Museum, Copenhagen; NRS, Naturhistoriska Riksmuseet, Stockholm; UMZC, University Museum of Zoology, Cambridge.

STRATIGRAPHY

The Upper Devonian in East Greenland outcrops in a number of localities surrounding Kejsers Franz Josephs Fjord, an area about 500 miles north of the Arctic Circle on the East coast. Outcrops occur on Ymers Ø on the slopes of Celsius Bjerg, along the slopes of Sederholms Bjerg in Paralleldal, and around the mountains of Gauss Halvo, including Smith Woodward's Bjerg, Stensiös Bjerg, and Wimans Bjerg. The stratigraphy was described by Säve-Söderbergh (1932, 1933, 1934), Jarvik (Johansson) (1935), Büttler (1961), and has been amplified by the work of Friend *et al.* (1983). Nomenclature in this paper follows the latter work (Table 1).

The Upper Devonian System in East Greenland can be divided into three major groups. The Kap Kolthof Group underlies the Kap Graah Group, dating from the Frasnian through to the Lower Middle Famennian, the latter being equivalent to the *Phyllolepis* Series of Säve-Söderbergh. These are overlain by the Mount Celsius Supergroup which completes the Upper Devonian strata of the area. The Mount Celsius Supergroup in turn is divided into two groups, the lower *Remigolepis* Group which is equivalent to Säve-Söderbergh and Jarvik's *Remigolepis* Series, and the upper

TABLE 1

Friend et al. (1983)			Säve-Söderbergh - Jarvik (1935)		
Mt. Celstus Supergroup	Grönlandaspis Group		Arthrodire Sandstone Series		600m
	*Britta Dal Formation	Remigolepis Group	Remigolepis Series	Upper Reddish Division	550m
	Wimans Bjerg Formation			Middle Grey Division	200m
	*Aina Dal Formation			Lower Red Division	80m
Kap Graah Group		Phyllolepis Series		1700m	

*Tetrapods

Grönlandaspis Group equivalent to Säve-Söderbergh and Jarvik's Arthrodire Sandstone Series. It is from the former Group that the tetrapods derive.

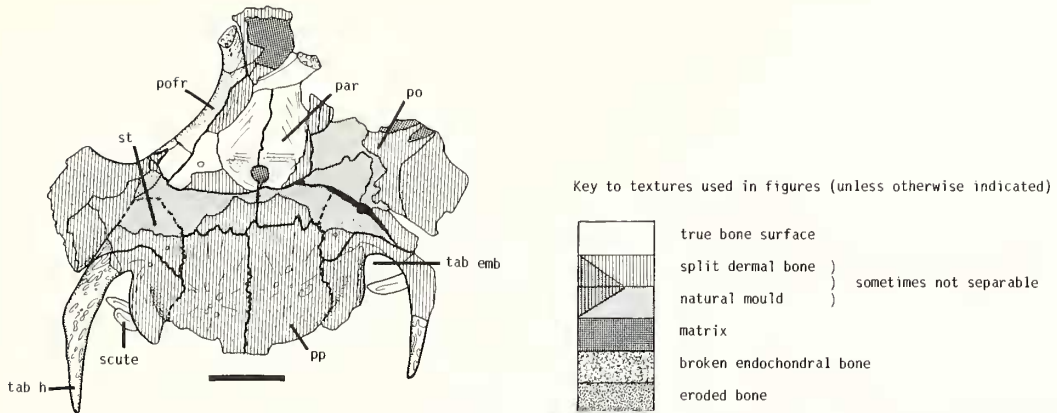
The *Remigolepis* Group consists of three distinct formations which can be recognized over the whole area, though the three vary in thickness. The lower Aina Dal Formation, equivalent to Säve-Söderbergh and Jarvik's Lower Reddish Division, consists of red coarse- and medium-grained siltstones and has yielded a rich fauna including many specimens of *Ichthyostega*. It reaches a maximum thickness of 80 m on Gauss Halvø, where it passes smoothly into the grey siltstones of the Wimans Bjerg Formation, equivalent to Säve-Söderbergh and Jarvik's Middle Grey Division. This is essentially unfossiliferous. Its maximum thickness is 200 m and it passes into the upper Britta Dal Formation, equivalent to Säve-Söderbergh and Jarvik's Upper Red Division, which reaches its maximum thickness of 550 m on Stensiös Bjerg. This consists of red and grey siltstones and some red sandstones, and is interpreted by Nicholson and Friend (1976) as representing dominantly fluvial channel and floodplain sedimentation. It has also yielded a rich fauna including *Ichthyostega* and *Acanthostega*. The Upper Devonian sequence is terminated by the grey fine- and medium-grained sandstones of the *Grönlandaspis* Group, which reaches a maximum thickness of 600 m. As Friend *et al.* interpret it this sequence was originally of much greater thickness but was eroded during the Carboniferous Period. Friend *et al.* (1983) accept Jarvik's (1961) dating of the whole sequence based on the vertebrate fauna, and place the *Remigolepis* Group firmly within the Famennian. Spore analysis of rocks from several parts from this sequence was attempted by Friend *et al.* (1983) but all samples proved unproductive.

SYSTEMATIC PALAEOLOGY

Family ACANTHOSTEGIDAE Jarvik, 1952

Diagnosis of family. As for *Acanthostega*.

Type species. *A. gunnari* Jarvik, 1952.



TEXT-FIG. 2. *Acanthostega gunnari* Jarvik. UMZC T1300a-c, skull A, dorsal view, with interorbital region (exposed in ventral view) reversed and shown as transparent. Scale bar, 10 mm.

Diagnosis. Devonian tetrapod with skull table lacking intertemporal and with cheek-skull table junction spanned by arrowhead-shaped supratemporal. Tabular with deep embayment and long laterally developed horn; tabular-squamosal junction smooth. Postparietals relatively long, with convex posterior margin. Narrow interorbital region. Prefrontal large, excluding lachrymal from orbit. Nasals broad anteriorly; ?internasal present. Palate broad, closed, denticulate, small but evident interpterygoid vacuities, pterygoids meet anterior to cultriform process. Marginal palatal bones narrow, bearing numerous small teeth but ?no tusks. Parasphenoid grooved in mid-line; groove broadens between basipterygoid processes. Basipterygoid processes well developed. Otic capsules heavily ossified; ?roof of braincase closed. Simple abutment of braincase roof on to skull table; only small facet on tabular for attachment. Ornament groove and ridge, with some tubercular development; grooves often elongated near bone margins, in regions of growth, though this not invariable. Lateral-line canals in tubes through bone. Orbits circular to oval. Dentary teeth about seventy or more; maxillary dentition about forty-six; premaxillary dentition ?about twenty.

DESCRIPTION

Skull

Dermal Skull Roof. The new material substantially confirms and reinforces much of the information published by Jarvik (1952), but gives little further knowledge of areas such as the snout which were missing from the original material. It is unfortunate that the suspensorial region, difficult to interpret in the original specimens, is not represented in the new material, so that the presence or absence of a preopercular cannot be confirmed. Lacking also is any evidence about the shape and position of the external naris.

The unique horn and embayment, described by Jarvik (1952) in the original material, are major autapomorphies used to identify the new material as *Acanthostega*. In skull A the horns have both been exposed by mechanical preparation and show the unweathered bone surface to be ornamented dorsally (text-fig. 2). They are more substantial than those in either of the original specimens, both of the latter having suffered a certain amount of erosion. The holotype tabular horn shows a smooth mesial edge which was presumably embedded in soft tissue in life as Jarvik suggests, but this is not evident in skull A. Where the tabular meets the supratemporal and squamosal, it is thickened and is a substantial ellipse in cross-section, but further distally, where it becomes the tabular horn, it is flattened. The tabular-squamosal suture is simple and lacks interdigitations, the sutural surface of the tabular at this point is seen on the left horn of skull A, where there is no overlap surface at all for another bone. The lateral margin of the tabular turns mesially where it would have lost contact with the squamosal to become free tabular horn, but there is no evidence that it was embayed to correspond to the squamosal-tabular embayment of the holotype.

The question arises as to which of the two embayments of *Acanthostega* is the homologue of the 'otic' or 'spiracular' notch of other early fossil amphibians, which lies between the junction of the skull table and cheek regions. It is usually bounded by the tabular, and sometimes the supratemporal, dorsally, and the squamosal ventrally. At first sight, the lower of the two embayments in *Acanthostega* seems to fulfill these criteria. However, the state of the sutures bounding the tabular and contacting the squamosal and supratemporal suggest an alternative hypothesis. It is possible that the tabular has in effect 'grown around' the site of the original embayment, sealing the primitive kinesis found at this point in fishes. Thus the tabular embayment encloses the notch which may have housed a persistent spiracle, and a second embayment was produced where the tabular has 'sprung away' from the margin of the squamosal to form the horn. The suture of the tabular and squamosal remained uninterdigitated, betraying its history as part of the kinetic mechanism, though it is not suggested that there was any movement here. This hypothesis requires more information on the nature of the tabular-squamosal embayment.

At the anteromesial corner of the embayment the tabular bears a tiny process on the ventral surface, seen in the counterpart of skull B (text-fig. 3C), which may have been a facet attaching to the braincase. Also in this specimen, it is clear that the tabular is penetrated by a canal running almost from the posterior margin, anteriorly, parallel to the mesial edge of the embayment. It can be seen both in section and in ventral view where some of the underlying dermal layer has been lost (text-fig. 7B). The canal can also be identified on the left side of the holotype, whereas on its right side, because of the way the bone is preserved, a partial section through the canal gives the deceptive appearance of a downwardly curving flange.

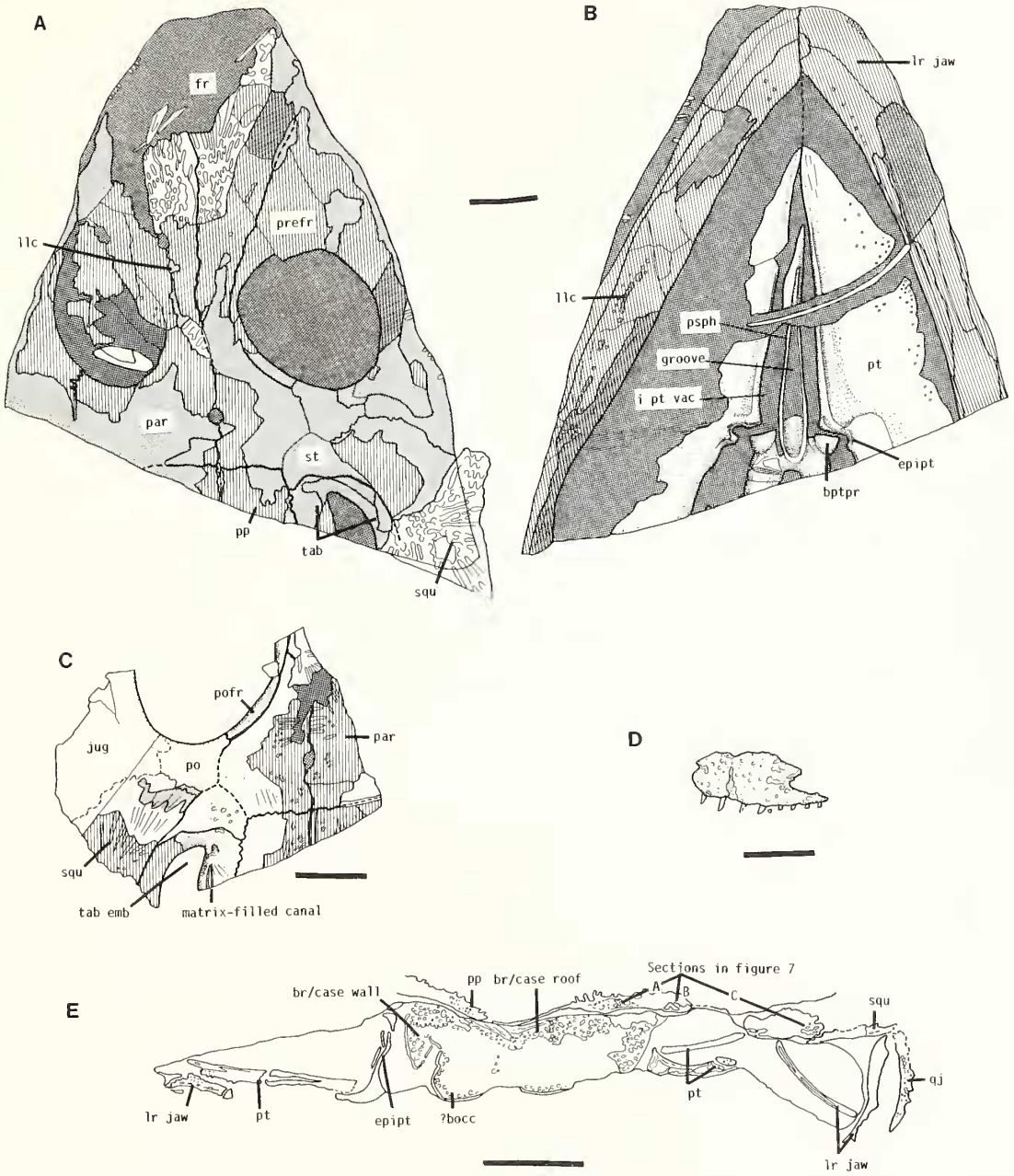
One of the most striking features in the skull table is the arrowhead-shape of each supratemporal, manifested particularly in the posterolateral and posteromesial corners, and seen best in an isolated skull table (text-fig. 6). This character is not as obvious in the original material since the sutures are difficult to trace, but it is consistent among the new skull table specimens. So characteristic is it that it can be used as a means of identification of incomplete skull table fragments. The posterolateral corner of the supratemporal is drawn out into a diminishing process 'squeezed' between the tabular and squamosal, until the latter meet in a butt-joint. This is particularly well seen in skull A, where the lateral margin of the tabular is well preserved.

The course of the squamosal-postorbital suture is rather difficult to establish in the new specimens of *Acanthostega*, resulting, apparently, from a substantial overlap on the inner surface between adjacent bones. Thus, internal and external views give a very different picture from one another and, where the bone is split horizontally, conclusions about the course of a suture can be quite contradictory. In the isolated skull table the postorbital appears to be a large bone, with an interdigitating suture with the squamosal at about the level of the apex of the tabular embayment. The specimen is exposed in internal view, but the bone is split, and the pattern it reveals is probably that of the external surface. On re-examination, the holotype shows a similar pattern. In the counterpart of skull B (text-fig. 3C), however, exposed also in internal view but with the bone here complete, what is apparently a good squamosal-postorbital suture defines a much smaller postorbital, the suture being positioned much further anteriorly than in the isolated example. Sutural overlap can be seen in the section through the counterpart of skull B, at the tabular-postparietal suture. Though quite clear in ventral view, in section a very thin lamina of bone from the postparietal lies on the ventral surface of the skull table, and it is the margin of this which is taken for the suture in ventral view (text-fig. 7A). The margin so formed follows the course which the suture would be expected to take, though no other evidence of the suture can be seen in the section. The same situation applies to the squamosal-postorbital suture of this specimen.

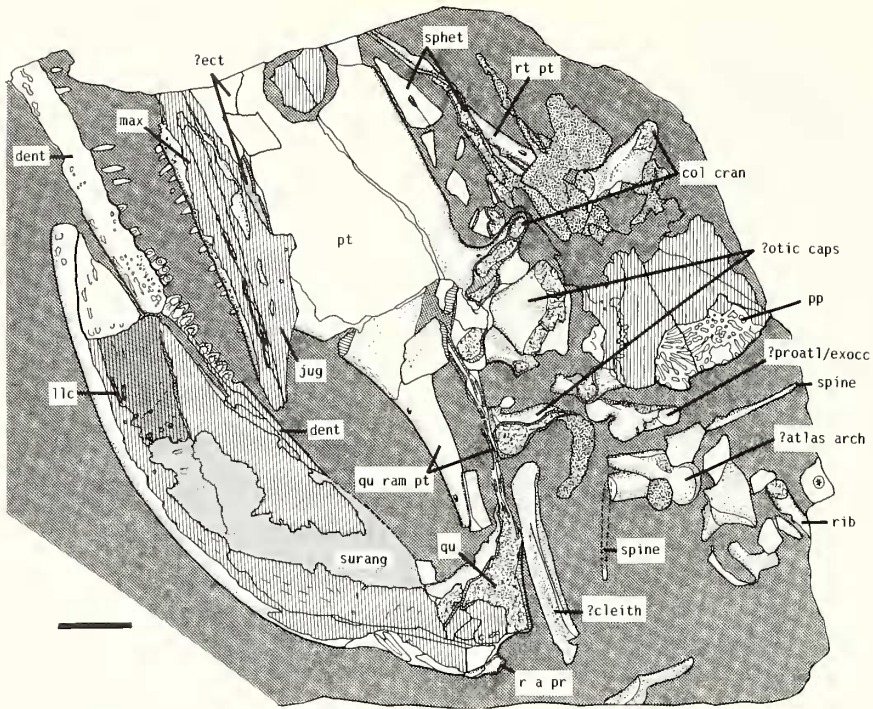
In all but one of the new specimens, the skull table is exposed in ventral view. Apart from that on the tabular, no other facets for support of the braincase have been identified, although the posteriormost parts of the postparietals are not preserved in ventral view in any specimen. In this respect, *Acanthostega* resembles *Ensthenopteron* and contrasts with *Ichthyostega*, in which there are complex facets under the whole of the postparietal. As in many other tetrapods the skull table is thickened in the region of the mid-line of the postparietals and parietals. Anterior to the parietal foramen in *Acanthostega*, the growth lines within the bone form a strongly transverse pattern, manifested as a thickened ridge in complete specimens.

Acanthostega resembled most other early tetrapods in the relatively small size of the otic region, judging from the proportions of the postparietals and parietals. *Ichthyostega*, with its apparently rather large otic region, was much more fish-like in this respect, as noted by Jarvik (1980).

The maxilla is preserved in skull C where it has remained in contact with bones of the palate, even though the dermal roofing bones are missing. This contrasts with the holotype, in which the maxilla lies apparently a little detached from the roofing bones. Jarvik (1980) interprets this to mean that it was independent from the roof. However, a more likely explanation is that it was sutured to them by a flat butt-joint similar to



TEXT-FIG. 3. *Acanthostega gunnari* Jarvik. A, UMZC T1300f, skull B, dorsal view (ornamented part of squamosal from T1300e). B, T1300f, skull B, ventral view. C, T1300g, counterpart of skull B, skull roof in ventral view. D, T1300g, isolated maxilla on reverse of specimen. E, T1300f, skull B, section through posterior part of skull. Scale bars, 10 mm.



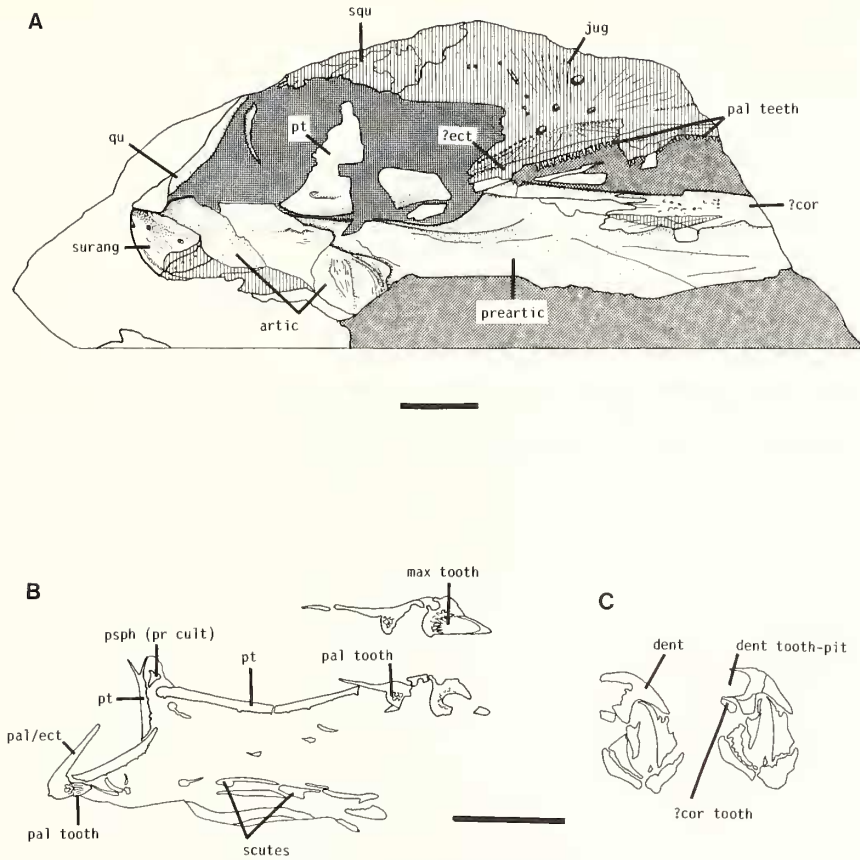
TEXT-FIG. 4. *Acanthostega gunnari* Jarvik. UMZC T1300j, skull C, dorsal view showing braincase, palate, left maxilla and lower jaw, and cervical elements. Scale bar, 10 mm.

that in embolomeres (Clack 1987), a structure which resists vertical forces during biting. The suture of the dentary to other bones of the lower jaw was of a similar form and can be seen in the section through skull C (text-fig. 5c).

An isolated premaxilla is preserved on the same block as the counterpart of skull B (text-fig. 3d). Surprisingly, it is narrow anteriorly and broadens towards the posterior end which is blunt and rounded. The anterior end shows an embayment presumably for accommodation of an internasal bone, found also in *Ichthyostega*, the loxomatids, and predicted for *Acanthostega* by Jarvik (1952) from the shape of the preserved frontals.

Dermal ornament is only preserved where it has not been exposed to weathering and has been prepared out mechanically. This includes areas on the frontals, nasals, and squamosal of skull B, and on the postparietals of skull C. Here it shows some difference from that of the second original specimen (GM A85) which is the only other specimen in which it is preserved. In the former, as in *Ichthyostega*, there are strongly radiating grooves and ridges present, the ridges often bearing raised tubercles, in contrast to the more 'honeycomb'-like arrangement of pits in A85.

Specimen A85 also differs in other ways from the majority of *Acanthostega* specimens. The posterior margin of the skull table between the tabular embayments is less markedly convex than in the holotype, and has a 'squared off' appearance. In those new specimens in which the posterior margin of the skull table is complete, the corners of the tabulars are gently rounded, and the posterior convexity is less marked than in the holotype. In A85 the postparietals appear relatively shorter than in other specimens altering the proportions of the skull table. Though the skull table width between the tabular embayments is roughly similar, the distance from the apex of the tabular embayment to the orbit is a little shorter in A85. It is also broader between the orbits. The differences cannot be taken to be taxonomically significant at this stage, since both possess the tabular horn and embayment definitive of *A. gunnari*. They must be regarded as individual variation unless discovery of further specimens shows otherwise.

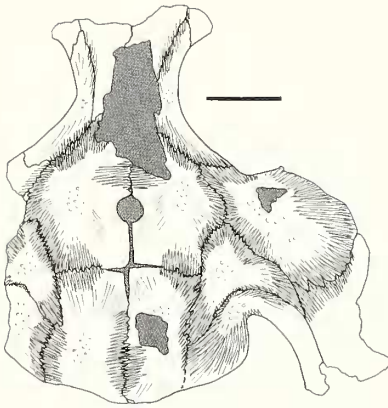


TEXT-FIG. 5. *Acanthostega gunnari* Jarvik. UMZC T1300j. Skull C. A, reverse of specimen, showing right side of cheek, right lower jaw. B, sections through anterior part of skull. C, sections through left lower jaw. Scale bars, 10 mm.

The new specimens show some size variation. The composite block contains two skull tables of identical size. These are significantly smaller than the holotype. An isolated specimen in which the skull table and horns are complete is intermediate in size between the holotype and A85. It has relatively short postparietals but resembles the holotype in interorbital width. Of two further isolated specimens, identified on supra-temporal shape, one is similar to the holotype and the other representative of by far the largest individual. As in other amphibians (*Proterogyrinus* Holmes 1984; *Archeria*, pers. obs.) the size of the parietal foramen varies unpredictably in different individuals.

Lateral-line canals are occasionally discernible in *Acanthostega*, as in *Ichthyostega*, running in tubes through the bones. They are difficult to detect in complete specimens, but are often more obvious in eroded ones where they can be seen in section, or as substantial canals infilled with matrix, or as a series of pores (text-figs. 3A, 4, 5A). They have been traced on the nasal, frontal, postfrontal, jugal, squamosal, and lower jaw. The canals and pores are difficult to distinguish from a second system which also leaves evidence of superficial foramina.

The dermal bones of *Acanthostega* have a middle layer penetrated by a complex interconnecting system of canals and tubules, which is responsible for the poor preservation of the bone. The bone usually splits through this weak layer, leaving the denser inner and outer layers on part and counterpart. Seen in section, the system of tubes and canals produces a network, in places so cavernous as to appear more space than bone. It may indicate that the bone was highly vascularized. The tubes are linked in places to pores on the outer and inner bone surfaces (text-fig. 7C). Where the outer ornamented layer has been removed, the



TEXT-FIG. 6. *Acanthostega gunnari* Jarvik. UMZC T1299. Isolated skull table. Stipple, matrix; dermal bone, split. Scale bar, 10 mm.

remnants of large vacuities can be seen, often in consistent places in different skulls, for example in the supratemporals of skulls A and B and the isolated skull table. The canal in the tabular appears to be part of this system. Without more and thinner sections of better preserved bone, it is not possible to elucidate the relationships of this pore system to that of the lateral-line systems. At first sight it resembles that described by Bystrow (1947) for *Benthosuchus*, though with a much more complex tube and pore system and without a *rete vasculosum*. Since the clavicle also shows the canals and pores, some connection with the vascular system is more likely than with the lateral line system.

Skull A shows a steep angle between the cheek and the skull table, rather greater than that in the holotype, but which is the more natural is hard to assess.

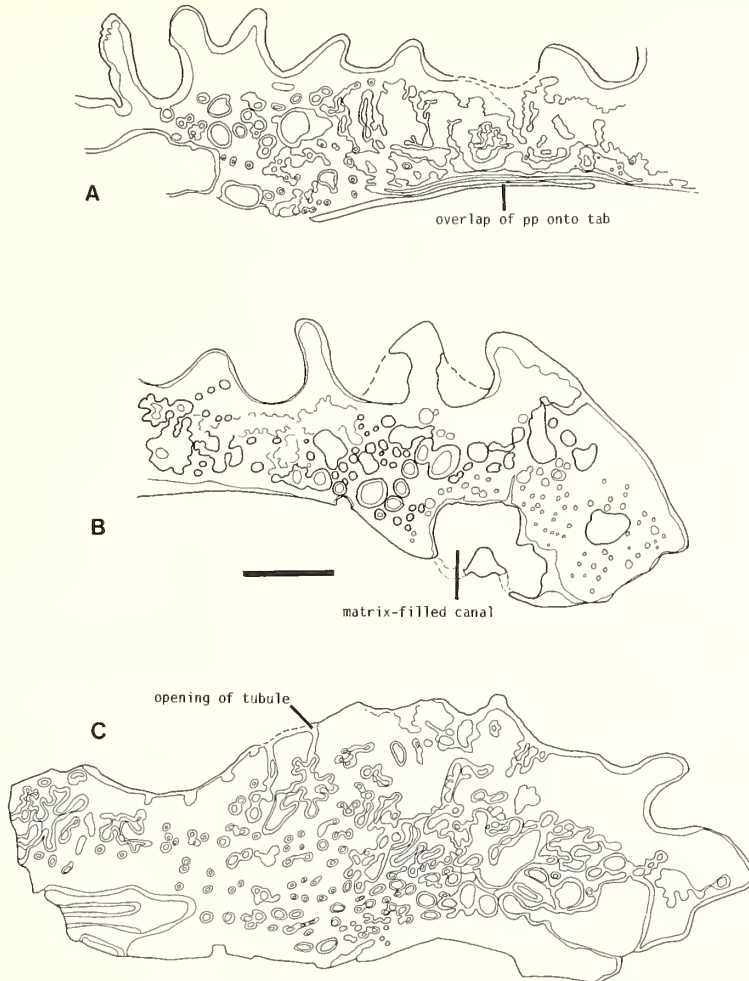
The right side of skull B shows an almost undistorted orbit which is effectively circular (text-fig. 3A). The right orbit of the holotype, by contrast, is somewhat elongated anteroposteriorly. Whether this difference is the result of the larger size of the holotype, or to its being compressed, is not certain.

Palate. The palate is visible in ventral aspect in skull B (text-fig. 3B), in dorsal aspect in skull C (text-fig. 4), in section through the posterior part (skull B) (text-fig. 3E), and anterior part (skull C) (text-fig. 5B).

There is a broad, almost closed, palate as in *Ichthyostega*, but with clear though narrow interpterygoid vacuities, bordered by the thickened mesial margins of the pterygoids, lying on either side of the parasphenoid. There was clearly no contact between the pterygoids and the parasphenoid at this point. This contrasts with the description which Jarvik (1980) gives of *Ichthyostega*, in which there are only tiny vacuities rather anteriorly placed at the front of the parasphenoid. Elsewhere, he figures the pterygoids as meeting the parasphenoid. However, Säve-Söderbergh (1932, pls. 4 and 8; pers. obs.) shows clearly that at least in some specimens of *Ichthyostega*, narrow interpterygoid vacuities did exist beside the cultriform process. Beyond the anterior end of the parasphenoid, the pterygoids met in *Acanthostega*, and may either have sutured or simply abutted each other. Lateral to the thickened mesial margins, the pterygoids are grooved in ventral view, especially posteriorly. Both the groove and the ridge fade as they pass anteriorly.

It is not possible to distinguish between the pterygoid and epipterygoid either around the basal articulation or on the quadrate ramus, though it is presumably the epipterygoid portion which forms the region accommodating the basiptyergoid process. This can be seen in ventral view in skull B, and is in essence like that of other early tetrapods with a peg and socket arrangement (text-fig. 3B). Just anterior to the basiptyergoid processes, the mesial margin of the pterygoid turns laterally through almost a right angle to form a posteriorly facing ledge. It is against this which the basiptyergoid processes appear to articulate, but this could result from compression having forced the pterygoids somewhat apart. The margin is then scooped out into a socket to accommodate the tip of the basiptyergoid process. The whole area surrounding the socket is thickened and the socket itself is bordered by a lip.

Posterior to the basal articulation, the quadrate ramus produces its ascending ramus, seen in section in skull B and in dorsal view in skull C. This was a thin sheet, much crushed in skull C, though in skull B, on the left side where the section is more anterior, the ascending ramus has remained intact. It reaches almost to the skull roof, where its dorsal margin is somewhat thickened. On the left it has been folded over and lies at a narrow angle to the horizontal (text-fig. 3E).



TEXT-FIG. 7. *Acanthostega gunnari* Jarvik. UMZC T1300f. Sections through dermal skull roof. A, through postparietal/tabular junction to show sutural overlap; B, through tabular system to show canal; C, through tabular to show tube system. Scale bar, 10 mm.

At the level of the basal articulation, in dorsal view in skull C, the thickened mesial margins of the pterygoid rise smoothly into vertical buttresses, where presumably they incorporate the epipterygoids and form the columellae cranii (text-fig. 4, 'col cran'). That on the left shows a smooth, rounded tip. On the right side of skull C, the columella cranii has been pushed laterally so that its mesial face is exposed, and a patch of unfinished bone at its base may represent part of the recess accommodating the basiptyergoid process, though it provides no useful detail.

The lateral margin of the subtemporal fossa has been exposed in skull C, and is robust and thickened. No muscle scars are apparent. The rounded margins of the fossa strongly suggests that the quadrate ramus of the pterygoid did not project below the level of the jaw margin as it does in some anthracosaurs such as *Palaeoherpeton* (Panchen 1964) and *Proterogyrinus* (Holmes 1984). In the section provided by skull B, this region of the pterygoid lies almost horizontal, though this skull is much compressed.

Most of the visible palate is formed by the pterygoids, denticulated on the ventral surface as in most other primitive tetrapods, but not described for *Ichthyostega*. The apparent absence of denticulation in *Ichthyostega*

may be simply a result of the type of preservation in which the true bone surface is rarely exposed. Small denticles would easily be missed when the bone splits through the spongy layer.

The marginal palatal bones have not been exposed in skull B, and only broken remnants remain in skull C. The latter does, however, show them in section at about the level of the posterior part of the palatine. This shows that at least the palatine overlapped the pterygoid internally to a marked degree, but that little would have been exposed in ventral view (text-fig. 5B). This contrasts with *Ichthyostega*, in which the marginal palatal bones are broad elements in ventral view.

The left quadrate of skull C is visible in section and is a substantial element with a considerable dorsal component. The posteroventral margin bears an embayment lying above the retroarticular process of the lower jaw, and was perhaps the site of attachment of a joint-stabilizing ligament (see below).

Parasphenoid and braincase. In skull B the braincase is visible in ventral view and in the oblique section which passes through the otic region (text-fig. 3B, E). A dorsal view of the much disrupted braincase of skull C is available where the dermal roofing bones have disappeared (text-fig. 4).

The parasphenoid is a long tapering element reaching anteriorly to a point about level with the front of the orbit. It does not contact the pterygoids, nor does it appear to continue above the point at which the latter meet each other. It is strongly ridged in the mid-line anteriorly, except for the first few millimetres, but as it passes back the ridge divides into two, enclosing a deep groove. The ridges diverge posteriorly for most of their length, but just anterior to the basal articulation they converge, and meet in a smooth curve just posterior to the basal articulation.

This form of parasphenoid has not been described in any other tetrapod. It most closely resembles that in some specimens of *Eusthenopteron* (e.g. NRS P6849A, pers. obs.) and *Megalichthys* (S. M. Andrews, pers. comm.). In these, however, the region between the ridges is denticulated, and pierced by a persistent hypophyseal foramen. In *Acanthostega*, the floor of the groove does not appear to be lined with periosteal bone, and is extremely difficult to prepare. Thus not all the matrix lying between the ridges has been removed. However, as far as it has, there is no evidence of either denticulation, or of a foramen. It is possible that the ridges represent the margins of a large gap in the dermal parasphenoid, with the floor of the chondrocranium visible above it. The hypophyseal fenestra appears to have closed, whereas the ossification of the parasphenoid was still incomplete. This could represent the retention of an embryonic condition, if the parasphenoid ossifies from paired centres as it does in *Sphenodon* and *Lepidosiren* (de Beer 1937). In other early tetrapods the parasphenoid is convex, usually with the strong mid-line ridge of the processus cultriformis in the hypophyseal region, and nothing is known about its development.

The parasphenoid sheathes the basiptyergoid processes as in other tetrapods, clearly separated from the more medial regions by smooth periosteal bone, but not by conspicuous carotid grooves as they are for example in anthracosaurs (*Palaeoherpeton*, Panchen 1964; *Eoherpeton*, Panchen 1975), and runs back from the basal articulation on either side. Just posterior to the point where the ridges converge, however, the bone is strongly depressed into a median concavity, apparently natural, but with the periosteal bone having a broken edge. If periosteal bone were present covering this concavity in life, it must have been very thin and thus not preserved. Alternatively, it was missing altogether. I am sufficiently confident of my preparation technique to believe that had it been preserved, it would have been found. Only further specimens could confirm the condition, but the implication of this specimen is that in *Acanthostega*, like *Ichthyostega* (Jarvik 1980; pers. obs.), the parasphenoid did not grow back to underlie the whole of the otic region. Thus *Acanthostega* would be only the second tetrapod to display this feature, otherwise only seen in primitive or paedomorphic fish.

Among the tetrapods, *Crassigyrinus* (Panchen 1985) appears most similar to *Acanthostega* in this region. In this animal, there was a large triangular concavity between and posterior to the basiptyergoid processes. It is in rather a different position relative to that of both the groove on the mid-line of the parasphenoid and the more posterior concavity of *Acanthostega*, and it is not clear to which of these that in *Crassigyrinus* would be homologous.

The basiptyergoid processes are tetrapod-like in being relatively large structures projecting laterally from the side-walls of the braincase. The articular faces lie with their anteroventral margins at approximately right angles to the parasagittal plane, but the shape of the articular surfaces is not known.

Both skulls B and C indicate that the otic region of the braincase was well ossified. Although skull C is much disturbed, there are clearly solidly ossified units which are best explained as otic capsules, though they are not interpretable in detail.

From skull B the section shows endochondral bone lying beneath the dermal bones, forming an ossified roof to the braincase. The underside of the skull table shows no significant facets attaching to the braincase,

so that the roof of the braincase would have made full but unsutured contact with the dermal skull roof over its whole surface. The situation is directly comparable to that in fishes such as *Eusthenopteron* (Jarvik 1980). It is in direct contrast to that in *Ichthyostega*, in which complex facets lie beneath the postparietal for attachment of the otic region, though the otic region itself is poorly ossified and difficult to interpret in the conventional pattern of either fishes or tetrapods (Jarvik 1980, pers. comm.; pers. obs.). Most other tetrapods in which the otic capsule is known to have an ossified roof, such as the loxommatids (Beaumont 1977), *Eoherpeton* (Smithson 1985), *Pholiderpeton* (Clack 1987) have more or less well-developed facets, especially on the tabular, for attachment of the braincase, in addition to smooth contact between the surfaces of braincase and skull table.

Laterally, the endochondral bone of the braincase roof descends to form the side wall, presumably of the otic capsule, with periosteal bone lining both lateral, ventral, and some of the mesial surface, seen on the left side (text-fig. 3E). This separates the upper part of the braincase well clearly from the more ventral parts, presumably formed from the basioccipital, and indicates the presence of a fenestra of some kind at this point. There is not enough evidence to describe this as a fenestra ovalis, though it is in about the expected position for one.

It has been suggested (Jarvik 1952) that the tabular embayment might represent an excavation of the skull roof lying above the equivalent of the fossa bridgei in the braincase. In *Eusthenopteron*, the fossa bridgei perforates the posterior wall of the otic-occipital unit, separating the paroccipital processes from the body of the braincase. Laterally the paroccipital processes contract the skull roof under the tabulars (terminology of Westoll 1943). Therefore, if the tabular embayment of *Acanthostega* is a dorsally open fossa bridgei, some contact between tabular and braincase would be expected lateral to the embayment. However, judging from the section afforded by skull B there appears to be none, with the embayments purely a character of the dermal skull roof. Other possible explanations for them are either that they were the site of attachment of axial musculature, developed in association with the elaboration of the tabular horn, or that they housed a persistent spiracle, as has been postulated for the 'otic notch' of *Crassigyrinus* (Panchen 1985).

Beneath the otic region, the basioccipital region can be seen as paired convex areas of endochondral bone with periosteal lining present laterally but fading to disappear in the mid-line. As described above, it is uncertain whether its total absence was natural or not. There appears to be no certain endochondral bone at this point in the mid-line, though it is difficult to distinguish from matrix, but its absence would accord with the presence of a persistent notochord running through the basioccipital as in *Ichthyostega*.

Lower jaw

Two skulls from the composite block have lower jaws in articulation. A further lower jaw specimen is associated with a humerus (see below) but cannot be attributed to *Acanthostega*. It is poorly preserved and offers little significant detail.

The left side of skull C provides the best-preserved lateral face of the *Acanthostega* jaws, though it is incomplete and the bones a little disarticulated anteriorly. The pattern of bones is that typical of a primitive tetrapod as far as can be ascertained. In one respect, however, it differs from the published account of *Ichthyostega*. In this form, Jarvik (1980) figures the dentary as running back to contract the articular, as it does in *Eusthenopteron*, but in no other described tetrapod. In *Acanthostega*, and also in the isolated lower jaw, the dentary terminates at about the mid-point of the adductor fossa, so that the surangular contributes to the margin of the fossa (text-fig. 4).

The dentary suture with the underlying bones (presumably coronoids, though none is well enough preserved to merit description) takes the form of a smooth shelf, a narrow flange descending laterally to meet the splenials (text-fig. 5C).

The lower jaw is not exposed in mesial view in any specimen, but the mesial components are exposed in lateral view on the right side of skull C. This shows clearly that the prearticular is a very large bone, as it is in *Ichthyostega*, and it passes as far anteriorly as the jaw is preserved (text-fig. 5A). It has a thickened ridge around the adductor fossa presumably for insertion of adductor musculature. The lower border is missing, precluding description of the suture with the splenials and the state of any Meckelian fossae. Portions of the disrupted coronoids lie along the dorsal border of this element.

The articular is exposed where the lateral components of the lower jaw are missing and it passes anteriorly to about the level of the middle of the adductor fossa. The articular surface is not exposed in any specimen. Posteriorly the surangular wrapped around the articular leaving none exposed dorsally as far as preserved. Both the left lower jaw of skull C and the isolated specimen show a small retroarticular process on the surangular, which may well have attached by a ligament to the quadrate to stabilize the jaw-joint as in *Proterogyrinus* (Holmes 1984).

Dentition

Marginal teeth are preserved best in skull C where they have been exposed by preparation. As in the holotype, they are almost even in size, though diminishing towards the rear of the row. They are simple cones, slightly recurved at the tips, and of oval cross-section with the long axis orientated bucco-lingually. Sections show that there was infolding of the enamel at the root of each tooth, but not in the exposed crown. Maxillary and dentary teeth show few differences, except for the slightly larger size of dentary teeth seen in skull C.

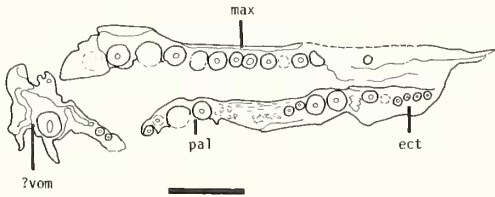
Tooth counts are difficult to estimate since the dentigerous bones of skull C are incomplete, and in skull B the maxillae are missing while many of the dentary teeth are missing or obscured by matrix.

The teeth in the maxilla of skull C, as exposed by preparation, apparently alternate regularly with spaces, while those in the dentary are in places closely spaced. In skull B, where visible, the teeth are also very closely packed, with ten to thirteen teeth per centimetre. A conservative estimate of the dentary tooth count, given a dentary length of 7 cm, would be about seventy. This is rather more than the maxillary count of the larger holotype, which is about forty-six (including spaces). The significance of this must await the discovery of further specimens.

The isolated premaxilla (admittedly only tentatively assigned to *Acanthostega*), shows remains of nine teeth with spaces for a further seven or eight. A premaxilla with a total of around twenty teeth would account for the difference between the dentary count of skull B and the maxillary count of the holotype.

Coronoids are not well represented in the specimens from site G920 and there is no firm evidence of coronoid teeth. Skull C shows a section of the left lower jaw in which a possible coronoid tooth is preserved (text-fig. 5c), but this could be a broken and displaced fragment of dentary tooth.

There are dentigerous fragments among the isolated specimens from G920, of which some show closely spaced teeth and some in which teeth alternate regularly with spaces. These and the identified specimens are in accord with the studies of Roček (1986), in which both replacement patterns can occur in both *Eusthenopteron* and *Ichthyostega*.

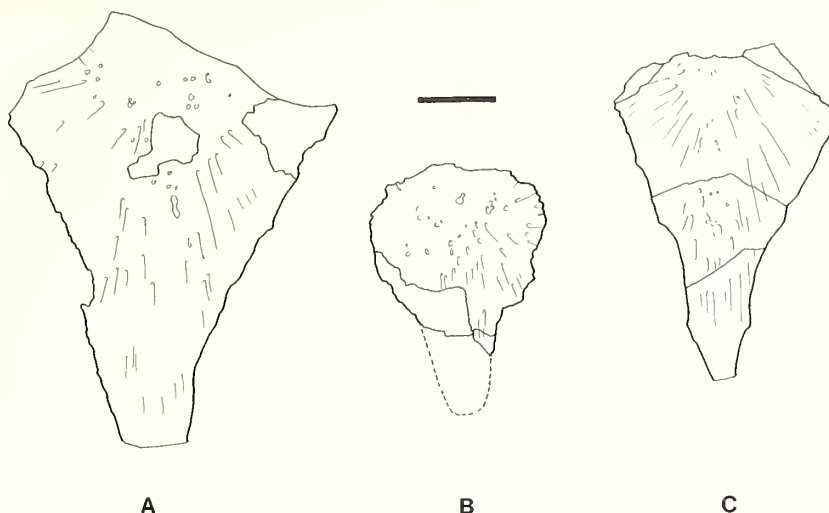


TEXT-FIG. 8. Greenland Geological Survey specimen GM A88, section through right dentition, in dorsal view. Scale bar, 10 mm.

Palatal teeth are not exposed in skull B, but are visible in skull C on the right side and in section. They are uniformly small, much smaller than the maxillary teeth, and on the exposed length there are about twenty-seven. This arrangement of palatal teeth is unusual among early tetrapods. Typically, the vomer, palatine, and ectopterygoids carry large tusks, often occurring in a pair in which one tusk is functional, the other being represented by a replacement pit. *Loxommatids* (Beaumont 1977), and the early anthracosaurs *Eoherpeton* (Panchen 1975) and *Greererpeton* (Smithson 1982) all show this pattern, and it is also found in osteolepiform fishes such as *Eusthenopteron* (Jarvik 1980). However, in the latter case, the palatal bones also carry a row of small toothlets lateral to the tusks, similar in number and arrangement to the toothlets seen in *Acanthostega*. What cannot be stated with certainty at this stage is that *Acanthostega* did not also carry a more mesial tusk-row. There is no evidence of it in the section, but it remains possible that the section failed to pass through such teeth on either side. However, the small ventral exposure of the lateral palatal bones which the section reveals suggests that the small toothlets were the only teeth present.

Jarvik (1980) states that *Ichthyostega* also lacked palatal tusks, and in the figures given by Säve-Söderbergh, only the vomer consistently shows teeth at all. Jarvik's reconstructions show a row of small teeth running the length of the marginal palatal bones, in this case about six on the ectopterygoid, seven on the palatine, and four on the vomer. Clearly this is different from the pattern in *Acanthostega*. However, among the specimens from G920 is an isolated tooth-bearing element in which one large tusk and a tusk pit is followed by four smaller teeth. On current evidence it belongs neither to *Acanthostega* nor to *Ichthyostega*.

Specimen GM A88, collected in 1947 by the Danish Swedish expeditions, from the south side of Celsius Bjerg, shows the natural mould of a denticulated palate in which the marginal dentition is still present, exposed in dorsal view sectioned across the tooth roots (text-fig. 8). On the reverse side of the specimen, the



TEXT-FIG. 9. Interclavicles. A, UMZC T1293, isolated specimen. B, T1300a, b, associated specimen. C, T1292, isolated specimen. Scale bar, 10 mm.

lower jaws are almost in life position. This clearly shows a palatal formula in which there are both tusks and smaller teeth on ectopterygoid, palatine, and vomer, though the vomerine teeth are not well preserved. The palatal tooth formula would be expressed thus: vomer2(2+) palatine(2)2 ectopterygoid(2)2+(6) in which bracketed numbers indicate small teeth, unbracketed, tusks.

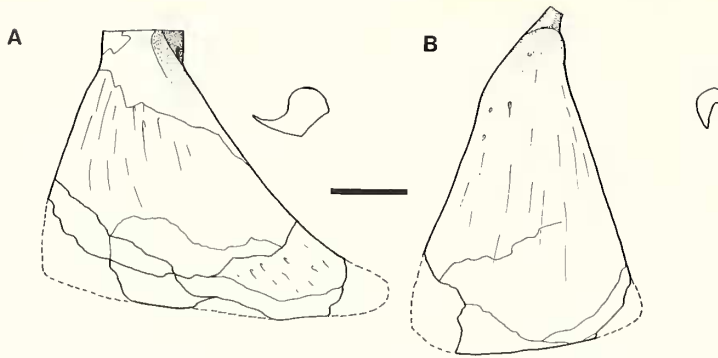
The maxillary teeth of this specimen are likewise exposed in section across the roots, and in the whole length of the maxilla there are nine teeth preserved with spaces for a maximum of twelve. The anterior teeth are much larger than the posterior ones. The tooth row is about 7 cm, about the same as that of skull B. There are perhaps a maximum of seven teeth in the premaxilla. Eighteen teeth are exposed in the dentary, with spaces for a further eight, unless the teeth are actually alternating with space, which does not seem to be the case. Thus the complete marginal tooth count for this specimen would be about twenty-six to twenty-eight per side.

In summary, specimen A88 is quite different in tooth formula from *Acanthostega*, and also from *Ichthyostega* as described by Jarvik. It is possible that this unknown form is also present at site G920, and contributed the isolated palatal element described above. It represents a third, as yet unnamed and undescribed species of tetrapod from the Upper Devonian of East Greenland.

Specimen GM A90 from Wimans Bjerg appears to have a similar dentary tooth count to skull B in a tooth row of comparable size, and might be attributable to *Acanthostega*, though it is associated with an ichthyostegan type of clavicle.

Pectoral girdle

Interclavicle. Three interclavicles are preserved (text-fig. 9). One is closely associated with skull A in the composite block and may confirm the identity of the two isolated elements from the same site. All three interclavicles are kite-shaped and resemble those of the anthracosaurs *Pholiderpeton* (Clack 1987), *Proterogyrinus* (Holmes 1984), and the temnospondyl *Dendrerpeton* (Carroll 1967). They are quite different from that of *Ichthyostega* which has a long parallel-sided posterior stem very like that of *Seymouria* (White 1939). This suggests a different adaptation of the pectoral girdle from that in *Ichthyostega*. Kite-shaped interclavicles are more often found in aquatically adapted animals and long-stemmed ones in more terrestrially adapted ones, though the correlation is not invariable (Clack 1987). Unfortunately, none of the *Acanthostega* interclavicles has an adequately preserved external (ventral) surface, so that neither the form of the ornament nor the region of clavicular overlap can be ascertained. It has been assumed that the broader portion of the bone would have been anteriorly placed as in embolomeres, rather than the more tapering portion as in colosteids. The largest specimen is preserved with its internal (dorsal) surface moderately well preserved and this is smooth and featureless.



TEXT-FIG. 10. Clavicles. A, UMZC T1300*d, e*, associated specimen. B, T1294*a, b*, isolated specimen. Sections through stems figured to right of specimen, mesial surface figured uppermost. Scale bar, 10 mm.

Clavicle. Three clavicles are preserved, two associated with the composite block. One of these has the blade preserved chiefly in section, with a little of the stem visible, but it supplies little useful information. The second shows most of the blade and a little of the stem. The third is on an isolated block and is complete except for the tip of the stem. These two clavicles are rather different from one another (text-fig. 10).

In that associated with the composite block (text-fig. 10A), the angle between the anterior and posterior margins is about 60° . The base of the stem is supported by a stout buttress internally, with a smooth groove running up the anterior margin, and the section available reveals that the posterior margin was also grooved. If the true mesial edge is as preserved, the blade would have been a triangle with its posteromesial edge a right angle. The angle between the anterior and posterior margins of the isolated example (text-fig. 10B) is about 40° , giving the blade the shape of an isosceles triangle. Its stem appears rather slender, judging from the section available and though it is in hard crystalline matrix and difficult to prepare, no evidence of a groove along the anterior margin can be found.

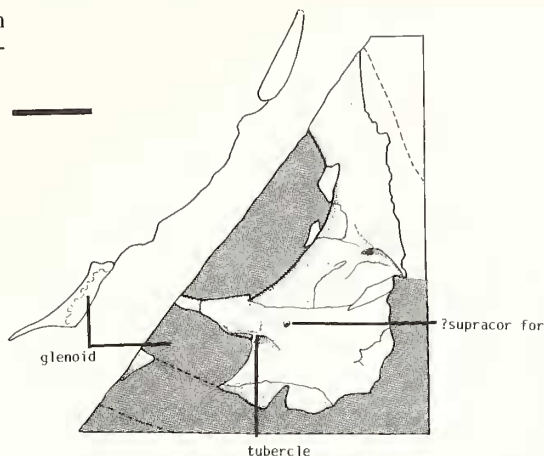
This isolated element compares closely with that illustrated by Jarvik (1980) for *Ichthyostega*, and may indicate that this genus was also present at site G920. The associated example may be assignable to *Acanthostega*.

Cleithrum. A cleithrum has not been positively identified, but a bone associated with skull C (text-fig. 4) may represent one. A long narrow bone lies along the preserved margin of the right quadrate ramus of the pterygoid, its free end eroded, the other obscured by possible braincase elements. The bone preservation suggests endochondral rather than dermal bone, but if it is not a cleithrum, the bone is not identifiable at present. The bone is an almost parallel-sided strut, with a deep groove along the dorsally exposed face, which tapers out as the bone runs forward beneath other parts of the skull.

Scapulocoracoid. This is preserved in association with skull C, exposed in lateral view, the anterior margin obscured by overlying bones (text-fig. 11). Given the lack of disturbance of other postcranial elements associated with skull C, this bone can be assigned to *Acanthostega* with moderate confidence. The ventral margin, having been poorly ossified in life, becomes increasingly difficult to distinguish from matrix and has not been completely exposed. A section passing through the scapular region and the posterior part of the glenoid shows that the bone below the glenoid is very thin.

Like those of most other early tetrapods, this scapulocoracoid shows a substantial ossification of the scapular region, though it is narrower than most. It contrasts with that of *Ichthyostega* in which no endochondral scapular region is found, its place being occupied by the large dermal cleithrum. The posterior margin of the scapulocoracoid curves strongly and smoothly to form almost a full semicircle, similar to that seen in the embolomere *Pholidroperon* (Clack 1987). It is thickened especially in the supraglenoid region, but no supraglenoid foramen, such as is usually present in early tetrapods, has been found in the exposed part. There is a very small foramen situated beneath a curving ridge running anteroposteriorly across the bone at approximately the level where the scapular region merges into the coracoid region (text-fig. 11). It is unlikely to be equivalent to the supraglenoid foramen of other tetrapods.

TEXT-FIG. 11. Scapulocoracoid, UMZC T1300j, with section through bone, associated with skull C, orientation uncertain. Scale bar, 10 mm.



The orientation of the glenoid is unknown, as is its shape and surface form. At its anterior end, the glenoid is supported by the stout supraglenoid buttress which forms a tubercle at the anterodorsal corner of the glenoid. A thin flange of bone runs above the dorsal margin of the glenoid as far as preserved. Just anterodorsal to this tubercle there is another small foramen, possibly equivalent to the supracoracoid foramen of other early tetrapods (for example, *Archeria*, Romer 1957), but in a rather different relative position (text-fig. 11).

In summary, though there are differences in detail between this scapulocoracoid and that of other tetrapods, as far as preserved it is much more typical of the tetrapod pattern than is that of *Ichthyostega*.

Other postcranial elements associated with skull C

Fragments of three ribs lie in association with skull C, approximately in life position, but very little information can be gained from them. One shows a flange developed on the anterodorsal margin, but it is very different from the massive overlapping ribs developed even in the cervical region of *Ichthyostega* (Jarvik 1952).

There are cervical elements associated with skull C, again more or less in life position, but the preservation makes interpretation very difficult (text-fig. 4). One element may be an atlas arch, another a pro-atlas (or perhaps a disarticulated exoccipital). Two slender spines (probably a pair) were present (one now removed and preserved separately), one on each side of the vertebral column, which may have been atlantal ribs. Atlantal ribs are not usually found in early tetrapods, and these would represent a primitive feature.

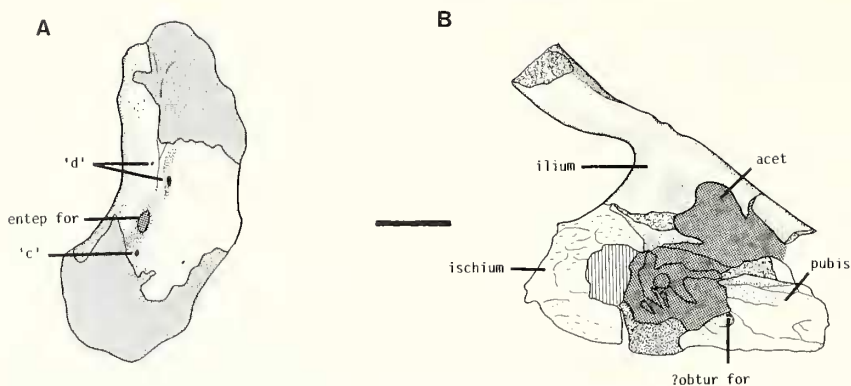
Beneath skull B lies a very thin curved bone. It has blunt ends and is featureless. It cannot be identified as belonging to any known fish, and may be interpreted as part of the hyoid apparatus or other parts of a vestigial gill support system.

Numerous scutes lie in the composite block, particularly associated with skull C. They are narrowly oval, with a pronounced ridge along one edge which varies in height among the scutes.

Isolated humerus

A poorly preserved humerus (text-fig. 12A) is associated with a lower jaw from site G920, but attribution of either to *Acanthostega* cannot be made at this stage. However, it will be described because it shows some differences from that described by Jarvik (1980) for *Ichthyostega*. All that remains of the bone substance is the internal surface of its thin perichondral lining seen in ventral view. The rest of the outline is preserved as a natural mould which renders little detail. There is no evidence on the surface of the radial condyle, situated ventrally in *Ichthyostega*, though since the outer layer of bone is gone, this is not conclusive evidence of its absence here. Nothing useful remains of the other articular surfaces.

The bone is kidney-shaped, with the entepicondyle arising in a gentle curve from the shaft of the bone, at an even more obtuse angle than in *Ichthyostega*. There may have been some distortion during diagenesis, since the entepicondyle lies almost in the same plane as the shaft of the bone. Some degree of torsion between the two would normally be expected in a primitive tetrapod humerus, as in *Ichthyostega*. It has an anterior flange, as in the humeri of primitive tetrapods such as *Proterogyrinus* and *Greererpeton* (Holmes 1980), in



TEXT-FIG. 12. A, humerus, UMZC T1295, untextured portions represented by thin shell of eroded endochondral bone. B, pelvic girdle, T1291. Scale bar, 10 mm.

that of *Ichthyostega* as reinterpreted by Panchen (1985), and apparently in that of *Tulerpeton* (Lebedev 1984). The ectepicondyle is unfortunately not visible.

The humerus possesses an entepicondylar foramen situated in the usual place for tetrapod humeri, and it also shows accessory foramina. There are two foramina equivalent to those labelled 'd' by Jarvik (1980) in the humerus of *Ichthyostega* and also in that of *Crassigyrinus* (Panchen 1985), but otherwise unknown in tetrapods, and one equivalent to the 'c' foramen in *Ichthyostega* which is not found in *Crassigyrinus*. In *Ichthyostega*, the 'd' foramina lie either side of a ridge which runs obliquely across the bone from Jarvik's 'process 6' about half-way along the length of the bone, to terminate at the posteromedial corner of the entepicondyle. In the humerus from G920, a ridge, which is probably equivalent, runs down from the head of the bone parallel with the shaft, and merges into the margin of the entepicondyle. This appears more similar to the position of the 'd' foramina in *Crassigyrinus* than in *Ichthyostega*.

This humerus, though unidentified and poorly preserved, is significant for two reasons. First, it shows the humerus of a second genus of tetrapod from the Upper Devonian of East Greenland, other than *Ichthyostega*. Jarvik (1952) mentioned the existence of an 'Eryops-like' humerus in the material collected from East Greenland during the Danish-Swedish expeditions, but he does not now believe this to be so (pers. comm.). Secondly, this humerus shows that the primitive foramina found in the humerus of *Eusthenopteron* (Andrews and Westoll 1970) are now known in at least three species of primitive tetrapod.

Isolated pelvic girdle

Like the humerus, this element (text-fig. 12B) cannot be attributed to *Acanthostega*, but will be described because it too shows substantial differences from that of *Ichthyostega* (Jarvik 1980). The left half of the girdle is exposed in lateral view, and is preserved more or less intact. The anterior and ventral margins are incomplete and were probably poorly ossified in life. The tip of the postiliac process has been broken off. It is not possible to be sure whether the element was ossified as a unit or as three separate ossifications, since there are breaks across the regions where these sutures might be expected.

The ilium was well ossified and has a substantial postiliac process directed posteriorly, with its dorsal margin at an angle of approximately 25° to the ventral margin of the element. This contrasts with *Ichthyostega* (Jarvik 1980) in which these two margins are almost parallel. The process broadens distally, and the section available is a narrow oval orientated dorsoventrally. A more significant difference from the ilium of *Ichthyostega* is in the complete absence of an iliac crest. Instead, the dorsal margin slopes anteroventrally, and two very slight processes arise above the base of the postiliac process. These may indicate where the sacral rib attached, though without an internal view, it is impossible to be sure. In this respect this pelvic girdle resembles that of temnospondyls, such as that attributed to *Dendroperpeton* (Carroll 1967), and those of *Amphibamus* (Carroll 1964) and an as yet undescribed specimen from the Lower Carboniferous of Scotland (UMZC T1261). The girdle attributed to *Baphetes* (the 'Pictou Girdle': Watson 1926; Panchen 1970) also apparently lacked an iliac crest. Microsaur pelvic girdles vary greatly, some with iliac crests (e.g. *Ricnodon*) and some without (e.g. *Hylloplezion*) (Carroll and Gaskill 1978). All known anthracosaurs, such as

Proterogyrinus (Holmes 1984) and *Eoherpeton* (Smithson 1985), have a large iliac blade arising dorsally and in this respect resemble *Ichthyostega*.

The body of the ilium is thickened to support the acetabulum, with an anteroventrally directed buttress above it which terminates in unfinished bone. A more complex region lies posterior to the acetabulum, where an almost hemispherical depression imparts a lobed shape to its posterior margin. As preserved, therefore, the acetabulum is essentially heart-shaped. The lobed region may be equivalent to that in *Eoherpeton* (Smithson 1985) where a supra-acetabular notch is interpreted as the site of a ligament attaching to the femur.

The posteroventral portion of the acetabulum is supported on what appears to be a thickened horizontal buttress, but this could well be an artefact caused by compression. The surface of the acetabulum is not visible; as in other parts of this material, unlined endochondral bone is almost impossible to distinguish from matrix. The acetabulum lies much further anteriorly in the ilium than it does in most other tetrapod pelvic girdles. Typically, the acetabulum lies directly beneath the point at which the postiliac process arises.

The ischium is relatively thin, but quite well ossified except at the margins. The posterior margin has a similar hatchet shape to that of *Ichthyostega*. The pubic region is similarly preserved, but the anterior margin is incomplete. It is not obvious what, if any, contribution the pubis made to the acetabulum. It is possible that the whole unit was continued more anteriorly in cartilage. Only one small foramen pierces the pubic region of this pelvic girdle, which is difficult to interpret as an obturator foramen.

In *Ichthyostega*, the pubic region appears very truncated as illustrated by Jarvik (1980), though he notes that the anterior margin was cartilage-finished. In examining the specimens of the pelvic girdle of *Ichthyostega*, I found one which appears to show a long, rather narrow and poorly ossified pubis, with large obturator foramina, in articulation anteriorly. It seems as though the whole pubis remained largely cartilaginous and was only rarely preserved. This could well have been the case in the 'Pictou Girdle', in which the pubic region appears to be even more truncated than in *Ichthyostega*.

While the pubis in early tetrapods was apparently the last element of the pelvic girdle to ossify, and is often not preserved, in the pelvic girdles of osteolepiform fishes (Andrew and Westoll 1970; Jarvik 1980), there is a single ossification which is generally homologized with the pubis of tetrapods because it is anteriorly directed. The contrast suggests that close homologies between the two elements may not be possible. It seems more likely that the element in osteolepiform fish is homologous with those in other fish groups, where homologies with the tetrapod girdle are not evident.

DISCUSSION

The new material of *Acanthostega* reveals, as Jarvik (1952) suspected, an animal quite different from the better-known *Ichthyostega*, and if the postcranial elements are correctly assigned to *Acanthostega*, the differences are known to extend to the postcranium. This serves to emphasize what has become apparent from more recent finds of Devonian tetrapods, that by the late Devonian, tetrapods had radiated widely both in space and ecologically, and that the emergence of tetrapods occurred much earlier than the late Devonian.

Although the new specimens of *Acanthostega* are so incomplete, they nevertheless provide evidence of both similarities and differences between it and *Ichthyostega* which contribute to the debate, not so much about the origin of tetrapods or their relationships to any fish group, but of what primitive tetrapods were actually like, in other words, what were the primitive characters of tetrapods, and which of them were tetrapod autapomorphies. Most of these, like the majority of those cited by Gaffney (1979), are directly related to overcoming the problems of life on land.

Historically, since the work of D. M. S. Watson (especially 1926), the embolomeres (in which group Watson included the loxommatids), were considered to be the most primitive tetrapods, both because they were the earliest tetrapods known at the time, and because they showed resemblances to the osteolepiform fishes from which they were considered to have emerged. These tetrapods were all late Carboniferous in age, by which time it is now known that the group had undergone a considerable radiation, possibly explosive in character. As Devonian tetrapods become better known, it may become clearer which characters shown by Carboniferous forms were actually primitive, thus which characters may legitimately be taken to represent tetrapods as a whole in the debate about their closest relatives. In searching for the true primitive state of a character,

evidence from neither stratigraphy nor functional morphology can be ignored. Panchen and Smithson (1987) and Schultze (1987) have recently used a combination of both these lines of evidence in a debate about which characters are true autapomorphies of lungfishes and can be used to represent them in a cladistic analysis, as distinct from those which characterize a subgroup (albeit the majority) which arose subsequently.

The differences between *Acanthostega* and *Ichthyostega*, as shown by the new evidence, include the ossification of the otic region and its relationship to the skull roof, a character of the lower jaw, and those seen in the postcranial skeleton. Similarities include the broad, closed palate, and the lack of any skull table-cheek kinesis, though the pattern of skull table bones is quite different in each. Possibly similar also is the presence of an internasal bone and a persistent ventral otic fissure and notochordal basioccipital, though the evidence for these is less certain.

Among the similarities between them, none yet discovered can be considered as indicating any special relationship, that is, a synapomorphy which unites them more closely to each other than to other tetrapods. By the same token, neither shows any synapomorphies which could unite it with any other early tetrapod group. The material is still too imperfectly known to warrant any more detailed discussion of the possible relationships of *Acanthostega* to other tetrapods.

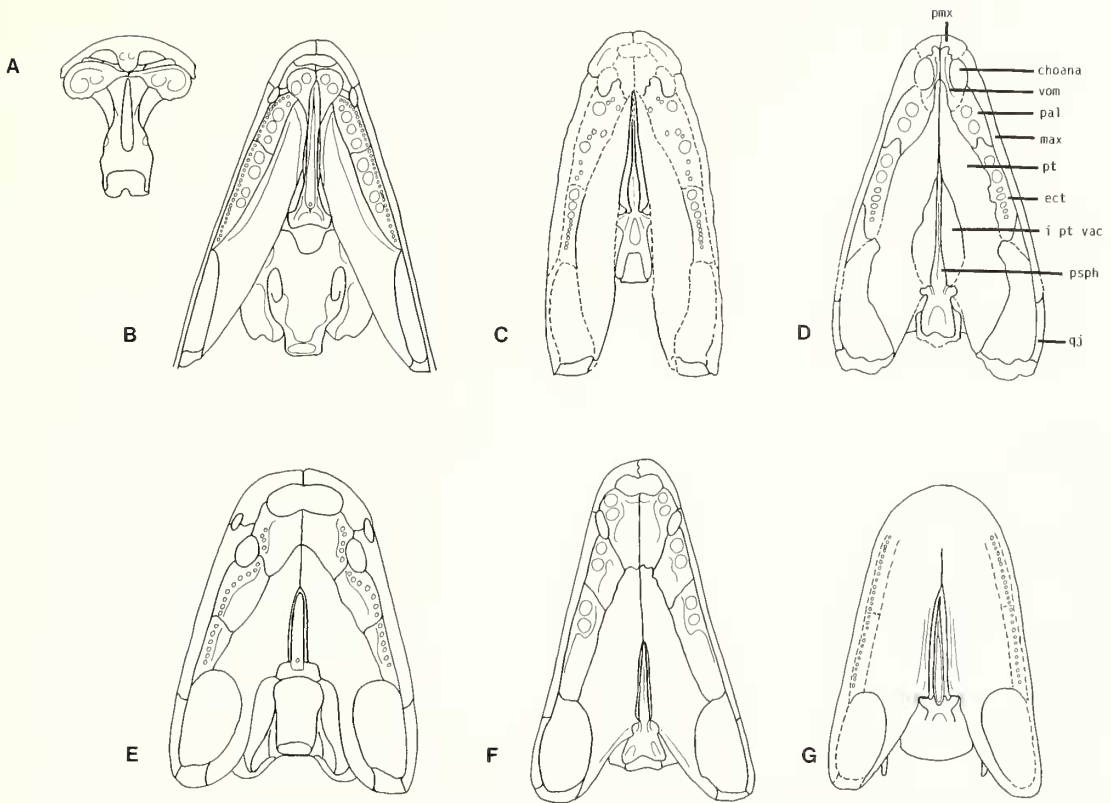
The closed, plate-like palate of *Ichthyostega*, in which the parasphenoid sutured to the pterygoids laterally, has been considered a unique feature of the genus (Jarvik 1980), though this has also been seen as a character uniting tetrapods with lungfishes by Rosen *et al.* (1981). They saw it as similar to the palate in lungfishes, where a short broad parasphenoid sutures along its length to the pterygoids. In some respects, however, the palate of *Ichthyostega* shows primitive characters, and one of these is the suture between the pterygoids anterior to the parasphenoid. This character has been considered primitive for tetrapods since Watson (1919, 1926).

My examination of the palate of *Ichthyostega* convinces me that the parasphenoid was separated from the pterygoids by narrow but distinct interpterygoid vacuities, as in other primitive tetrapods. In *Acanthostega*, narrow interpterygoid vacuities were certainly present, and again the pterygoids met anteriorly. The isolated specimen from Celsius Bjerg, A88, clearly neither *Acanthostega* nor *Ichthyostega*, also shows a broad, closed, and somewhat dorsally convex palate, though there is no evidence concerning the relationship of the parasphenoid to the pterygoids.

Among the better known Carboniferous groups, the pattern in these Devonian forms is most closely matched by that in the loxommatids (Beaumont 1977). In other forms, interpterygoid vacuities, though still narrow, are nevertheless significantly larger, and the anterior suture between the pterygoids more restricted, allowing the parasphenoid a longer ventral exposure. Anteriorly, the pterygoids are also generally narrower. These features can be seen in the colosteid *Greererpeton* (Smithson 1982), *Crassigyrinus* (Panchen 1985), and the embolomeres *Proterogyrinus* (Holmes 1984) and *Pholiderpeton* (as '*Eogyrinus*', Panchen 1972; Clack 1987). It is this form, rather than the closed loxommatid palate, which has usually been considered primitive for tetrapods, primarily because of its apparent similarity to that of osteolepiform fishes, in particular that of *Eusthenopteron* (text-fig. 13).

The presence of the broad, closed plate-like palate in each of three Devonian forms and in the loxommatids presents a *prima facie* case for consideration of this pattern, rather than that of embolomeres, as primitive for tetrapods. What are the implications of this?

Seen in ventral view, the area about the mid-line of the palate seems very similar in embolomeres and osteolepiforms, with narrow pterygoids, long narrow interpterygoid vacuities, and a long exposure of the parasphenoid, but the similarities may be more apparent than real. In *Eusthenopteron*, on either side of the parasphenoid, the pterygoids descend to form a strongly vertical component. This creates the illusion of narrow pterygoids and narrow, but real, interpterygoid vacuities, similar to those of embolomeres. In fact there is only a very small gap between the parasphenoid and the pterygoids. The vertical component of the pterygoids can be seen clearly in section (Jarvik 1980), and this results from the fact that in primitive osteichthyan fish both head and body are laterally compressed, consequent upon their streamlined fusiform shape, an adaptation for aquatic locomotion. It remains true among recent forms that, in general, tetrapods are



TEXT-FIG. 13. Palates of fishes and early tetrapods (marginal dentition omitted). A, *Osteolepis macrolepidotus* (anterior part only); B, *Eusthenopteron foordi*; C, *Crassigyrinus scoticus*; D, *Pholidropteron scutigerrum*; E, *Ichthyostega* sp.; F, *Megalocephalus pachycephalus*; G, *Acanthostega gunnari*. (A, B, E, after Jarvik (1980); C, after Panchen (1985); D, after Clack (1987); F, after Beaumont (1977); G, original.)

dorsoventrally compressed as compared with the lateral compression common in fish. Thus the broad, closed palate of these Devonian forms could result from dorsoventral flattening of a palate like that of an osteolepiform.

The resemblance between the palate of the embolomeres, *Crassigyrinus*, and *Eusthenopteron*, may be associated with a secondary adaptation to aquatic locomotion and subsequent deepening of their skulls.

At the anterior end of the palate, the resemblances between any early tetrapod and osteolepiform fishes, in particular *Eusthenopteron*, are less obvious (text-fig. 13). Two character differences are of interest here. In all the earliest tetrapods so far discussed, the pterygoids meet anteriorly, whether it be in a sutural contact or simple abutment. In no osteolepiform is this so. In *Eusthenopteron*, the pterygoids are separated along their length by the parasphenoid, and this seems to have been true of all osteichthyans except lungfishes. One of the characteristic differences between fish and tetrapods is the elongation of the snout in the latter. This not only influenced the bones of the dorsal part of the skull around the naris and the orbit, but also, it seems, of the underlying palate, causing the pterygoids, but not the parasphenoid, to lengthen anteriorly and meet in the mid-line. Though lungfishes exhibit the same pattern, it was clearly not derived in association with elongation of the snout, since it is also present in short-snouted forms (Miles 1977).

The second character to be considered is the relationship between the pterygoids, vomers, and parasphenoid. In the early tetrapods discussed so far, the vomers meet in the mid-line anteriorly,

though in most, with the exception of the loxommatids *Megaloscephalus* and some specimens of *Baphetes* (Beaumont 1977), and in *Acanthostega* in which the condition is not known, they are separated posteriorly by anterior extensions of the pterygoids. In *Eusthenopteron*, by contrast, the vomers are separated throughout most of their length by the parasphenoid, while the pterygoids lie lateral to both. It is difficult to see how the tetrapod pattern could be derived from this rather specialized condition. The osteolepidids, however, show a condition closer to the primitive sarcopterygian pattern in having vomers which barely meet in the mid-line, their common junction meeting the anterior tip of the parasphenoid. Elongation of the snout could more easily have produced the tetrapod pattern from this than from the eusthenopterid condition (text-fig. 13). Panchen and Smithson (1987) have recently argued that eusthenopterids rather than osteolepids form the sister-group of tetrapods.

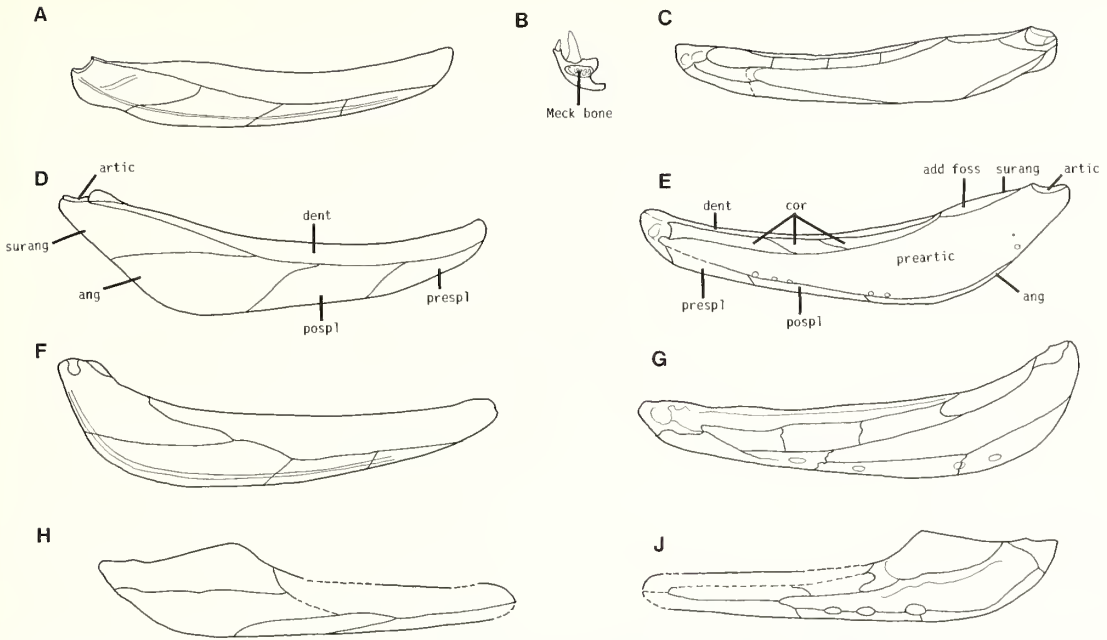
In neither *Ichthyostega*, nor *Acanthostega*, nor the loxommatids, all of which show the broad closed palate, is there any sign of the skull table–cheek kinetism found in fish, associated with movements of the cheek and opercular region during ventilation and feeding, which is usually assumed to have its homologue in the straight, unconsolidated suture found in this region in, for example, embolomeres, *Eoherpeton* (Smithson 1985), and *Crassigyrinus* (Panchen 1985). On the same basis used for consideration of the palate, is it justifiable to consider the consolidated skull as primitive for tetrapods?

Movement between the skull table and cheek bones in osteichthyan fish is necessary to accommodate the expansion of the gill chamber during the ventilatory cycle. However, it is characteristic of tetrapods that the opercular series is all but lost; when gill breathing was superseded by other methods of ventilation it became unnecessary. Gill breathing in adults would have been eliminated at an early stage in tetrapod evolution. In the dorsoventrally flattened skulls of Devonian tetrapods, the appropriate movements of the cheek would have been difficult to achieve. However, particularly in a dorsoventrally flattened skull, there would have been some benefit to eliminating the weakness at the skull table–cheek junction. It is significant in this context that in *Ichthyostega*, *Acanthostega*, and the loxommatids, the result has been achieved in different ways, and so presumably by convergent evolution. Only the loxommatids retain the pattern of bones in the skull table which comparison with osteolepiforms suggests to be primitive, retaining the intertemporal at least in early members of the group.

Why then did embolomeres, *Eoherpeton*, and *Crassigyrinus* apparently have a 'kinetic' skull roof reminiscent of that of osteolepiform fish? It has been suggested (see Clack 1987) that the 'kinetism' in these forms was rather the result of development of a butt-joint between the horizontal skull table and the steeply sloping cheek, which enhanced resistance to compressive forces during jaw closure. Perhaps, like the palate, the similarities to osteolepiforms are associated with secondary deepening and lateral compression in the skulls of these animals. Embolomeres and *Crassigyrinus* were secondarily aquatic, though apparently *Eoherpeton* was not. The condition is derivable from that of an early loxommatid, and it is the latter, rather than the embolomere pattern, which may represent the true primitive condition for tetrapods. This hypothesis would be supported if further finds of Devonian tetrapods show dorsoventrally flattened skulls with broad palates, and would be more satisfactorily refuted by the discovery of an early tetrapod with an undeniably flattened skull which was nevertheless 'kinetic', rather than a steep-sided skull with no 'kinetism'.

Consideration of the differences between *Ichthyostega*, *Acanthostega*, and other tetrapods, has highlighted three characters of which one is a true tetrapod autapomorphy, and two may be autapomorphies of all tetrapods other than *Ichthyostega* ('Neotetrapoda', Gaffney 1979).

1. Differences between the interclavicles of *Acanthostega* and *Ichthyostega*. The differences may well be caused by differences in the functional morphology of the rest of the skeleton, and how well adapted it was for terrestrial locomotion, but this will be hard to assess until more of the postcranium of *Acanthostega* is known. However, the possession of a large dermal interclavicle exposed ventrally between the clavicles, and bearing ornament, appears to be characteristic of early tetrapods. It is probably associated with both protection of the thorax and elaboration



TEXT-FIG. 14. Lower jaws of fishes and early tetrapods (dentition omitted). *Eusthenopteron foordi*: A, lateral view; B, section through anterior end; C, mesial view. *Ichthyostega* sp.: D, lateral view; E, mesial view. *Megalocephalus pachycephalus*: F, lateral view. G, mesial view. *Eoherpeton watsoni*: H, lateral view; J, mesial view. (A-E, after Jarvik (1980); F, G, after Beaumont (1977); H, J, after Smithson (1985)).

of the pectoral musculature in terrestrial locomotion. It contrasts with the small interclavicle of *Eusthenopteron*, a form in which the interclavicle is known. In most early sarcopterygian groups, the interclavicle is not known, suggesting that it was also small or absent altogether. It was present as a small element in primitive actinopterygians and could represent an apomorphy of osteichthyans (Gardiner 1984). However, an interclavicle bearing dermal ornament and large with respect to the clavicle, is found only in tetrapods and may be cited as a tetrapod autapomorphy, resulting directly from adaptation to terrestrial locomotion.

2. Differences in the relationships of the dentary to the articular between *Ichthyostega* and *Acanthostega*. As figured by Jarvik (1980), the dentary of *Ichthyostega* runs along the whole of the dorsal margin of the lower jaw, to contact the articular. This pattern is found in *Eusthenopteron* and many other sarcopterygian fishes. It differs from that in *Acanthostega* and in all other described tetrapods, where the dentary is excluded from most of the dorsal margin of the adductor fossa by the surangular (text-fig. 14). Assuming Jarvik's description to be accurate, this represents an autapomorphy of all tetrapods other than *Ichthyostega*, and on this evidence the lower jaw of *Metaxygnathus* (Campbell and Bell 1977) appears to be a true tetrapod. Loss of contact between the dentary and articular could have been associated with elongation of the snout, characteristic of tetrapods, and in this respect it is surprising to find that *Ichthyostega* retains the fish-like condition.

3. A suture between the anterior coronoid and the presplenial on the mesial surface of the lower jaw, at the anterior end (text-fig. 14). *Ichthyostega* differs from all other described tetrapods in lacking this feature, although, unfortunately, *Acanthostega* yields no information on this. The presplenial curves round under the ventral margin of the jaw ramus to meet the anterior coronoid, forming a tube in cross-section enclosing the Meckelian space. Although the jaw associated with skull C appears tubular in cross-section (text-fig. 5c), the bones are disturbed and broken and the elements difficult to interpret.

In *Eusthenopteron*, and in other primitive sarcopterygian fishes, the presplenial ('anterior infradentary' in fish terminology) is essentially a flat bone in cross-section. Beneath the anterior coronoid lies a convex ridge formed by the Meckelian bone (seen in section in Jarvik's 1980, fig. 76 and reproduced here in text-fig. 14E), which may or may not be overlain on the mesial surface by the prearticular. It is difficult to be sure from his figure where the anterior suture of the prearticular lies. In *Ichthyostega*, the prearticular appears from his figure to pass along the complete length of the jaw ramus to the symphysis. In neither case, however, is there any contact between the presplenial and the anterior coronoid (text-fig. 14).

The typical tetrapod condition could have arisen by reduction of the Meckelian bone, a process that certainly occurred in tetrapods, where as a rule the only ossification of Meckel's cartilage to survive is the articular. Formation of a tubular cross-section at the anterior end of the lower jaw would have conferred greater stiffness to this element, and so would be more resistant to bending or twisting forces than the fish jaw. It would represent a more economical use of materials: a tetrapod jaw of this design would be stiffer than a fish jaw of the same mass, or the same stiffness could be achieved for less mass. The difference could represent fundamental differences in the musculature of the jaws in the two groups in which there may have been lateral forces produced by the jaw muscles of tetrapods which were not experienced by fish.

A presplenial-anterior coronoid suture may thus be cited as a further apomorphy of neotetrapods, again explicable in terms of the demands of terrestrial life. As described by Campbell and Bell (1977), *Metaxygnathus* is a true neotetrapod on this character, though the specimen is very poorly preserved (A. L. Panchen, pers. comm.).

It would be of great interest to know the state in *Elpistostege* (Schultze and Arsenault 1985) of each of these three characters and also to know the pattern of the palatal bones. The second lower jaw character could be confirmed quite easily by a section across the anterior end of the skull, which might also yield some information about the relations of the pterygoids, vomers, and parasphenoid.

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ABBREVIATIONS

acct	acetabulum	pmx	premaxillary
add foss	adductor fossa	po	postorbital
ang	angular	pofr	postfrontal
artic	articular	pospl	postsplenic
bocc	basioccipital	pp	postparietal
bptpr	basipterygoid process	preartic	prearticular
br/case	braincase	prefr	prefrontal
clav	clavicle	prespl	presplenic
cleith	cleithrum	proatl/exocc	proatlas or exoccipital
col cran	columella cranii	psph	parasphenoid
cor	coronoid	psph (pr cult)	processus cultriformis of parasphenoid
dent	dentary		
ect	ectopterygoid	pt	pterygoid
entep for	entepicondylar foramen	qj	quadratojugal
epipt	epipterygoid	qu	quadrate
fr	frontal	qu ram pt	quadrate ramus of pterygoid
i/clav	interclavicle	r a pr	retroarticular process of lower jaw
i pt vac	interpterygoid vacuity		
jug	jugal	rt pt	mesial margin of right pterygoid
llc	lateral-line canal	scapcor	scapulocoracoid
lr jaw	lower jaw	sphet	sphenethmoid
max	maxilla	st	supratemporal
Meck bone	Meckelian bone	squ	squamosal
obtur for	obturator foramen	supracor for	supracoracoid foramen
otic caps	otic capsule	surang	surangular
pal	palatine	tab	tabular
pal/ect	palatine or ectopterygoid	tab cmb	tabular embayment
pal tooth/teeth	palatal tooth/teeth	tab h	tabular horn
par	parietal	vom	vomer